Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

ON THE QUESTION OF AN ARBOREAL ANCESTRY OF THE MARSUPIALIA, AND THE INTERRELATIONSHIPS OF THE MAMMALIAN SUBCLASSES.

A REVIEW OF CERTAIN PHASES OF PRESENT AND PAST OPINION.

B. ARTHUR BENSLEY.

RECENT researches have seemed to indicate that the theory, proposed by Huxley, of a genetic succession of the former representatives of the Monotremata, Marsupialia, and Placentalia, is untenable, and have thus reopened the most fundamental question of mammalian zoölogy, as to the interrelationships of the primary subclasses and the possibility of a di- or polyphyletic origin.

The recent publication by Dollo ('**99**) of the results of his studies on the foot structure of the Marsupialia, which he interprets as confirming the growing idea of a placental origin of the group, renders this an opportune time to review and comment upon certain features of the evidence which has lately been produced in opposition to Huxley's theory.

I. THE EVIDENCE OF AN ARBOREAL ANCESTRY OF THE MARSUPIALIA AND ITS BEARING AS INTERPRETED BY DOLLO.

The question of arboreal ancestry is of considerable importance in determining the relationships of the Marsupialia, and Dollo's results may accordingly be reviewed in some detail.

On page 191 of his paper we find the problem involved set forth as follows:

"Car si cette étude démontre que les ancêtres immédiats des Marsupiaux étaient arboricoles, il sera prouvé, du même coup, que ces Mammifères ne peuvent représenter la souche des Placentaires.

"En effet, personne ne soutiendra que *tous* ceux-ci ont passé par une phase arboricole. Et quant à ceux qui en sont là aujourd'hui, ce sont des types sporadiques, qui ont pris naissance indépendamment : la chose est évidente.

"Si, donc, la nature du pied des Marsupiaux nous amène à ce résultat, que leurs ancêtres immédiats étaient arboricoles, cette conclusion contribuera à appuyer ce que nous ont appris le placenta et la dentition du lait, notamment :

"A savoir, que les Marsupiaux constituent un rameau latéral très specialisé, et non le groupe générateur des Euthériens actuels."

The essential element of Dollo's theme is therefore an attempt to prove, by means of the structure of the foot, that the Marsupialia are primarily arboreal animals and that in respect to the possession of an arboreally modified foot they are too specialized to have constituted the source of the Placentalia.

Dollo recognizes in the marsupial hind foot certain characters of arboreal adaptation. These are (*a*) opposability of the hallux, (*b*) predominance of the fourth digit, with reduction and syndactylism of the second and third, and (*c*) recession of the claws. These characters represent successive stages in the development and perfection of a prehensile foot. Their purpose is essentially that of placing the great toe in opposition to the outer digits, notably the fourth, in order to make the foot an efficient organ for grasping and holding fast to the limbs of trees.

For convenience Dollo considers the marsupials in two series, — those which have the great toe well developed and functional, and those which have it reduced, or atrophied. This division is naturally one of habit; the former are animals which have retained the arboreal habit, while the latter are animals which have abandoned it. In these the great toe, being no longer useful, has become reduced.

To the first series belong the American opossums (Didelphyidæ) and the Australian phalangers (Phalangeridæ). In the Didelphyidæ (Fig. 1, *a*), with the exception of the subgenera Micoureus and Philander, opposability of the hallux is

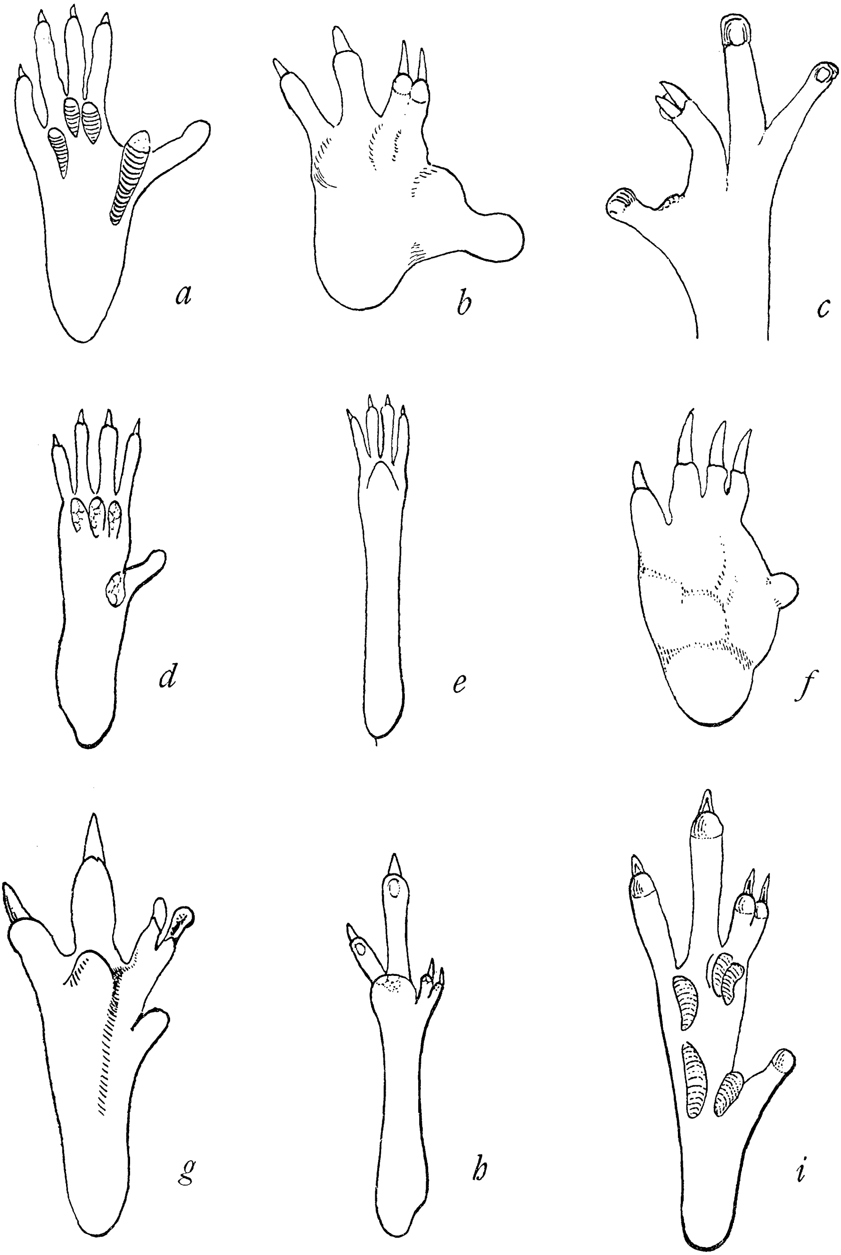


FIG. 1, *a–i.* — Schematic representations of the more important types of foot structure in the Marsupialia, as interpreted by Dollo.

a, *Didelphys nudicaudata*; *b*, *Phalanger celebensis*; *c*, *Tarsipes rostratus*; *d*, *Sminthopsis murina*; *e*, *Antechinomys laniger*; *f*, *Phascolomys ursinus*; *g*, *Perameles doreyana*; *h*, *Peragal eleucura*; *i*, *Hypsiprymnodon moschatus*. (After Dollo.) For explanation see text.

the only arboreal character presented, the other digits remaining normal. But in Micoureus and Philander there is, in addition to the opposability of the hallux, an enlargement of the fourth digit. In the Phalangeridæ (Fig. 1, *b*) there is superadded to both of these a reduction and syndactylism of the second and third digits.

One member of the Phalangeridæ, Tarsipes (Fig. 1, *c*), which is unique in many other respects, is the only marsupial presenting the latest stage of arboreal modification. Tarsipes shows, in addition to all of the arboreal characters of the typical phalangers, a recession of the claws of the fourth and fifth digits.

To the second series belong the remaining members of the Australian fauna, the dasyures and their relatives (Dasyuridæ), the wombats (Phascolomyidæ), the bandicoots (Peramelidæ), and the kangaroos and wallabies (Macropodidæ). These animals are mainly terrestrial, but they all show arboreal modifications of the foot.

The dasyures have a functionally tetradactyl foot, derived from a pentadactyl one by reduction of the hallux. Various stages of this reduction are illustrated in the family; *Sminthopsis murina* (Fig. 1, *d*), for example, shows a well-formed hallux, while *Antechinomys laniger* (Fig. 1, *e*) has none at all. Wherever the hallux is indicated, however, it is of the opposable type. As in the Didelphyidæ, this is the only arboreal character represented in the family.

In the wombats (Fig. 1, *f*) arboreal characters are more numerous. The hallux is here reduced to a tubercle, but its transverse position proves it to have been formerly opposable. In addition, there is a slight syndactylism and reduction of the second and third digits.

The bandicoots have a functionally monodactyl foot, derived from a pentadactyl one by an enlargement of the fourth digit and a corresponding reduction of the others, notably the first, second, and third. It shows all of the arboreal characters of that of the typical phalangers. The least departure from the phalangerine condition is seen in *Perameles doreyana* (Fig. 1, *g*), in which the only pronounced modification is a reduction of the hallux. The greatest departure from this condition is seen in *Peragale leucura* (Fig. 1, *h*) and in *Chœropus castanotis*, in both of which the hallux is entirely obliterated, the fourth digit greatly enlarged, and the remaining digits much reduced.

The exclusive predominance of the fourth digit in Chœropus Dollo regards as significant evidence of former arboreal habit, since in other cases in which there is a tendency towards monodactylism, as, for example, in the horse, it is not the fourth digit which predominates, but the third. The fourth digit must have been enlarged, and the third reduced, in the Peramelidæ, in connection with arboreal habit, before the tendency towards monodactylism appeared in connection with terrestrial, cursorial habit; so that the already enlarged fourth digit became still more predominant, while the third became still more reduced.

The kangaroos and wallabies also have a functionally monodactyl foot, resembling closely that of the bandicoots, and showing a similar range of modification. The musk-kangaroo (*Hypsiprymnodon moschatus*) (Fig. 1, *i*), for example, which is the most generalized type of the family, has a foot which, like that of *Perameles doreyana*, is but little modified away from the phalangerine condition. The true kangaroos, on the other hand, have an extreme monodactyl foot, like that of the higher bandicoots.

Dollo considers separately the South American form Cœnolestes (Epanorthidæ) and the Australian burrowing form Notoryctes (Notoryctidæ). With regard to the former he quotes the description of the foot given by Thomas, as "hallux short, clawless, and not properly opposable; other digits subequal, the fourth slightly the longest." He recognizes this case as doubtful, but thinks it entirely probable that Cœnolestes also is of arboreal derivation.

In Notoryctes, finally, he finds indicated predominance of the fourth digit, and reduction and syndactylism of the second and third. These characters, he states, have not been adaptively developed in connection with a burrowing habit because they are not found in other burrowing animals, such as the moles (Talpa and Chrysochloris). They point rather to a former arboreal habit.

Dollo accordingly finds in all of the Marsupialia examined a more or less extensive arboreal modification of the foot, and from this he draws the following conclusions:

All of the Marsupialia were at one time arboreal.

In the possession of a modified foot they are too specialized to have constituted the source of the Placentalia.

They are, on the other hand, *highly modified Placentalia, in which the placenta has been lost.*

They doubtless arose from *very primitive Placentalia, in which an imperfect placentation resulted in frequent accidents, such as premature birth, and it was probably to avoid these accidents that the placenta disappeared.*

According to this conception there would be four types of development in the Mammalia, as follows: (1) An oviparous condition in the Monotremata, and formerly in the Prototheria. (2) A viviparous condition, *in which the placenta has not yet appeared; found in none of the existing forms,* but formerly present in the Metatheria. (3) A viviparous condition, with placenta, in the Placentalia, and formerly in the Eutheria. (4) A viviparous condition, *in which the placenta has disappeared, in the Marsupialia.*

II. HUXLEY'S HYPOTHESIS IN THE LIGHT OF RECENT RESEARCHES.

In order to define clearly the position of Dollo and other investigators on the question of the relationships of the Mammalia, it is necessary to notice in some detail the view of Huxley as expressed in his famous paper of 1880, with which modern speculation on this subject may be said to have begun.

Huxley recognized three primary and, in a sense, hypothetical divisions of the Mammalia, which he designated as Prototheria, Metatheria, and Eutheria, these groups being represented at the present day by the Monotremata, Marsupialia, and Placentalia, respectively. The existing Monotremata and Marsupialia he regarded as highly modified away from their original types, but the most generalized of the existing Placentalia (Insectivora) as only slightly so. He recognized a genetic succession of Prototheria, Metatheria, and Eutheria, the Metatheria being intermediate with respect to the possession of certain prototherian and certain eutherian characters, among the former notably a non-placental allantois. To the Marsupialia, in passing from the purely metatherian condition, he assigned the adoption of the following special characters : a prehensile foot, associated with arboreal habit ; a marsupium ; a reduced milk dentition ; a foreshortened period of uterogestation.

Huxley therefore implied the following plan of succession : the Prototheria giving rise to the Metatheria, and becoming specialized as Monotremata ; the Metatheria, in turn, giving rise to the Eutheria, and becoming specialized as Marsupialia ; the Eutheria becoming specialized as Placentalia.

In opposition to this Dollo and others regard the Metatheria as giving rise to the Eutheria or primitive Placentalia, and the latter as giving rise, on the one hand, by retention of the placenta, to the modern Placentalia, and, on the other, by loss of the placenta, to the Marsupialia. Other investigators, notably Osborn, Hubrecht, and Seeley, recognize a separate origin of the main mammalian stems.

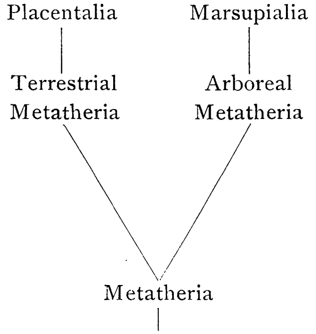
With this introduction we may examine certain features of the evidence on which these views are based.

1. *The Question of a Placental Origin of the Marsupialia.*

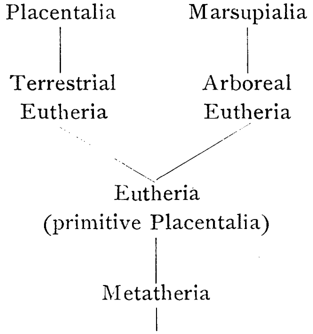
In the first place, what is the bearing of arboreal ancestry?

If we assign to arboreal habit any value as a differential character of the Mammalia, we may recognize two possible arrangements, based on the views of Huxley and Dollo, in which this factor might appear. For the sake of clearness these may be indicated in tabular form as on following page. According to the former plan arboreal habit would be associated with the differentiation of the Marsupialia and Placentalia. According to the latter it would also be an index — following Dollo — of a placental (eutherian) origin of the Marsupialia. This will make it clear that we have two distinct problems to decide: one as to the value of arboreal ancestry

HUXLEY.



DOLLO.



as an index of a placental origin of marsupials, the other as to its value as a factor of differentiation of marsupials and placentals.

For the solution of the former we have not far to seek. We may at once accept Dollo's statement that the ancestors of the Marsupialia were, in the possession of a modified foot, too specialized to have given rise to the Placentalia, because it is impossible to make any other assumption. In doing so, however, we do not in any way compromise Huxley's view; for it must be remembered that Huxley derived the Placentalia, not from Marsupialia, but from Metatheria. The prehensile foot he regarded as a special marsupial character. On the other hand, we cannot accept the evidence of arboreal ancestry as indicating a placental origin of marsupials. It scarcely needs to be observed that the assumption by non-placental Metatheria of an arboreal habit would account for, and in as satisfactory a way, the arboreal modifications of the foot which Dollo has demonstrated throughout the existing forms.

The latter problem yields much more satisfactory results. It is on this account, in fact, that Dollo's results have been considered in detail. If the former existence of an arboreal habit throughout the Marsupialia were susceptible of decisive proof,[1] we would have a fairly reliable index of the cause of the original separation of marsupials and placentals, because on a basis of arboreal habit we can explain the more important of the special characters which now distinguish the former. It is of interest to notice in this connection the opinion of Huxley: "I think it probable, from the character of the pes, that the primitive forms, whence the existing Marsupialia have been derived, were arboreal animals; and it is not difficult, I conceive, to see that, with such habits, it may have been highly advantageous to an animal to get rid of its young from the interior of its body at as early a period of development as possible, and to supply it with nourishment during the later periods through the lacteal glands, rather than through an imperfect form of placenta."[1] In other words, Huxley regarded arboreal habit as explaining two important characters of marsupials, namely the prehensile foot and premature birth. Now to these we may safely add the reduction of one of the dentitions, because, as Leche[2] has indicated, this is probably attributable to the peculiar suckling conditions which are brought about by premature birth. We may also add the marsupium; Klaatsch (**'92**) has shown that the perfect marsupium is a special character of the Marsupialia, and its perfect development in this group may best be explained on a basis of arboreal habit. Naturally these suggestions cannot be regarded as at all final, but they point strongly to an association of the special characters of marsupials with arboreal habit.

---

[1] I would regard the present evidence of arboreal ancestry as suggestive rather than as conclusive. Dollo has demonstrated conclusively that the Australian Marsupialia are of arboreal derivation, but a study of their characters, notably those of the teeth and feet, convinces me that they have arisen by a rapid adaptive radiation from opossum-like ancestors. If such is the case, they are not at

Passing by the results of Dollo, we find the idea of a placental origin of marsupials also expressed by Wilson and Hill (**'97**). These writers, in fact, originated this conception and produced what is perhaps the most significant evidence in its favor.

The valuable joint contribution of Wilson and Hill (**'97**) on the tooth development of Perameles, published in 1897, tended to confirm the idea, conceived by Huxley (**'80**), but elaborated

---

all representative of the Marsupialia in general. In the Jurassic fauna of the northern hemisphere, and the Miocene fauna of diprotodonts of South America, we have two important groups for which an arboreal habit cannot as yet be proven.

[1] Huxley (**'80**, p. 656).

[2] Leche. *Morph. Jahrb.*, Bd. xix, p. 525.

notably by Röse and Kükenthal,[1] of the former existence of a complete double dentition in the Marsupialia, and also indicated their tooth series as directly comparable to those of the Placentalia. Prior to this the permanent antemolar series of marsupials had been regarded as homologous not with the permanent series of placentals but with their milk series.[2] The results of Wilson and Hill seemed accordingly to suggest a fundamental relationship between the two groups in respect to dentition.

Similarly, the brilliant discovery by Hill (**'97**) of an allantoic placenta in Perameles, which was announced at about the same time, appeared to indicate a further relationship in respect to placentation, the Marsupialia having been previously regarded as entirely non-placental.

These writers in discussing the bearing of their results, although maintaining a moderate position throughout, recognized these resemblances as primary, and indicated their preference for a derivation of the Marsupialia, by retrogression both of milk dentition and placenta, from primitive Placentalia.

Now, although it must be admitted that decisive proof of a former diphyodont condition in the Marsupialia would be of considerable confirmatory value in the presence of other evidence, it would not of itself suggest placental origin. The possibility of such a condition was clearly perceived by Huxley in advocating the reverse. On page 655 of his essay he says: "I think that there can be no reasonable doubt that the existing marsupials have undergone a like suppression of the deciduous teeth, in the course of their derivation from ancestors which possessed a full set." Huxley, in fact, astutely realized that, in order to successfully derive the Marsupialia and Placentalia, it was necessary to assume the existence of a diphyodont condition in their metatherian ancestors.

We may accordingly pass over the evidence derivable from the tooth development of Perameles and consider in detail only that presented by Hill alone from a study of the placenta of this animal and the modifications of the allantois in other marsupials.

---

[1] See Wilson and Hill (**'97**, pp. 433–438).

[2] Röse, Kükenthal, Leche; see Wilson and Hill (**'97**, p. 582). This view has been recently supported by Dependorf (**'98**).

Prior to Hill's discovery of the placental allantois of Perameles, other investigators[1] had examined the modifications of the allantois in certain other forms. Owen, Selenka, and Semon had described for the phalangers (Phalangeridæ) and kangaroos (Macropodidæ) (Fig. 2, *c*) one condition in which the allantois was reduced and enclosed by the yolk-sac. Selenka had found a similar condition in the opossum (Didelphyidæ). Caldwell and Semon, on the other hand, had found in the koala (Phascolarctos) (Fig. 2, *b*) another condition in which the allantois was well developed and freely exposed to contact with the embryonic envelope, much as in the Reptilia.

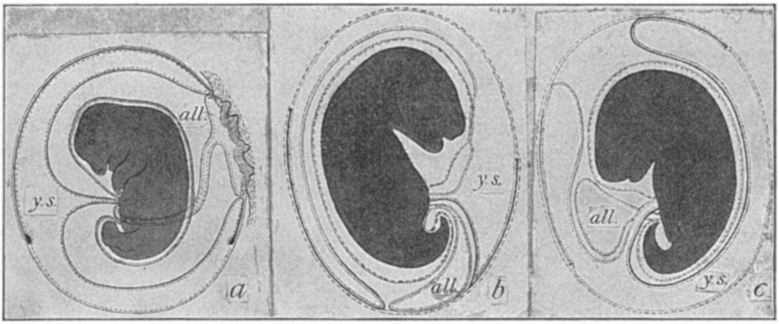


Fig. 2, *a–c*. — The main modifications of the marsupial allantois arranged in the order of their primitiveness as interpreted by Hill. (*b* may represent the type from which *a* and *c* have been derived.)

a, placental allantois of Perameles (from Parker and Haswell, after Hill); *b*, "respiratory" allantois of *Phascolarctos cinereus*; *c*, the reduced allantois of *Æpyprymnus rufescens* (Macropodidæ), (*b* and *c* after Semon); *y.s.*, yolk-sac; *all.*, allantois.

In his concluding remarks Hill considers these types and endeavors to decide as to which one of them is the most primitive; in other words, to determine whether a placental allantois is being developed secondarily in the Marsupialia, or whether the placental condition was formerly present throughout the group and has been subsequently lost in all forms (so far as known) but one.

He argues thus: that the reduced condition of the allantois is necessarily secondary; that although it is possible to derive the placental allantois of Perameles from one of non-placental type, like that of Phascolarctos, the reverse procedure is the more natural one, because Perameles is of more archaic aspect than Phascolarctos, and the latter is much more retrogressive in dentition; that it is entirely improbable that such a structure as an allantoic placenta should have developed twice independently in the Mammalia (*i.e.*, independently in Perameles). On these grounds he would regard the placental condition of the allantois as the primitive one for the Marsupialia and the non-placental allantois of most existing forms as secondarily derived by retrogression.

---

[1] See Hill (**'97**, p. 438).

That the typical condition of the allantois has arisen by reduction, and is therefore secondary, naturally admits of no reasonable doubt, for no one would suppose that the allantois would be incipient in animals which have passed through an oviparous phase. That the evidence derivable from the organization of the Marsupialia may be interpreted as proving a reduction of the allantois from a placental to a non-placental condition is, however, open to objection, both on general and on special grounds. In opposition we may maintain that there is no possible, and at the same time legitimate, way of assuming retrogression of the allantois on a basis of retrogression in other structures, especially those of adaptive character.

On general grounds, changes in the embryonic membranes may not be closely correlated with adaptive changes (progressive or otherwise) in the general organization. For example, the modifications of the placenta in placental mammals are not directly related to the adaptive (ordinal) characters of the animals in which they occur; several modifications may occur in the same group (*e.g.*, Edentata), a condition which may possibly be due, as Hubrecht[1] has suggested, to the greater youth of the placenta as compared with other structures of the animal organization, but which is more probably due to the fact that the allantoic placenta is not directly affected by the various evolutionary factors which determine the appearance of adaptive characters in the animal.

But even admitting such a correlation, retrogression of placenta could not be assumed on a basis of retrogression in single structures. For example, if we assume retrogression of the allantois from a placental to a non-placental condition on a basis of the more retrogressive character of the teeth of Phascolarctos as compared with those of Perameles, as suggested by Hill, we may also assume the reverse on the evidence of the feet, for, as Dollo has shown, the foot type of Perameles is a direct natural advance on that of Phascolarctos.

---

[1] Hubrecht (**'89**, p. 388).

The greatest objection, however, might be taken on the special grounds that the reduction and modification of the teeth which has taken place in Phascolarctos is not retrogressive ("decadent," Hill, p. 435) at all, but is, on the other hand, progressive and very comparable to that which has taken place in ungulate placentals; and, further, that as far as the greater primitiveness of Perameles or Phascolarctos is concerned there is little to choose; for although the former is decidedly more archaic in general dentition, its individual upper molar teeth are well evolved (quadritubercular), and its foot is much more specialized.

In all, it may be said that efforts to explain the reduction of the allantois, whether from a placental or non-placental condition, by reference to retrogression of the general organization are foredoomed to failure; for whatever may be true of the Marsupialia in general, the Australian members of the group, far from being degenerate, show a progressive adaptive radiation (doubtless made possible through freedom from competition) which parallels, and is in general very comparable to that which has taken place during the Tertiary period in placental mammals.

And in view of this a parallelism of placenta, though not genetically related to them, need not be more surprising than the extensive parallelisms in other structures. In other words, there is no adequate reason why the placental allantois of Perameles should not be regarded as *having arisen by progressive modification from one of non-placental* (*sauropsidan*) *type.*

These suggestions naturally do not imply that the placenta of Perameles is not primitive, or that in general the reduced allantois of the Marsupialia has not degraded from one of placental type, but that, as far as present evidence goes, the alternative view is just as plausible

The question now to be decided is whether or not the latter explains the facts of the case equally well.

Admitting the reduced allantois to be secondary, and recognizing the importance of the yolk-sac stage in marsupials, is it not just as probable that the reduced allantois has proceeded from one of sauropsidan type as that it has proceeded from one of placental type? A failure, due to whatever cause, of the allantois to form a placental connection furnishes a more plausible explanation of the premature birth of marsupials than that of Dollo (**'99**, p. 203), which attributes it to the loss of placenta in the violent gymnastics of an arboreal life. And it thus affords a simple explanation of the reduction of the allantois, inasmuch as premature birth, instituted through the failure of the allantois to form a placental connection, provides not only for the nutrition of the embryo but also for its respiration. This condition being perfected, the allantois, which is a provision for respiration during the later embryonic stages, having its function usurped, has naturally become reduced.

Why the allantois should have failed to form a placental connection cannot at present be explained. The question naturally suggests itself, Is not this also attributable to arboreal habit? It is not improbable that there may have been something in the assumption by metatherian animals of an arboreal habit which, for mechanical reasons, may have made a placental formation impossible.

While still concerned with the former relationships of marsupials, it is of interest to notice certain facts concerning their ancestry which have been derived from paleontology.

In a recent paper on the origin of mammals, Osborn (**'99**) has dealt with this subject and has represented in the form of a chart the probable geological and phylogenetic relationships of the mammalian subclasses. In this the Prototheria and Eutheria[1] are depicted as primary groups in the Triassic, the former appearing at a slightly later period than the latter. The Eutheria are depicted as giving rise, somewhere in the upper part of the Triassic, to the Marsupialia and Placentalia, which are represented in the Jurassic by the Triconodonta and Insectivora primitiva, respectively. The significant feature of this is the time relation which is implied by the recognition of marsupial and placental types among the Jurassic Mammalia.[1] If we may argue from the probable sequence of events, it would appear that we have an important clue to the characters of the Jurassic forms, namely the single tooth change of Triconodon, providing that the latter is comparable to that of existing forms. For if the reduction of one dentition is, as Leche suggests, attributable to premature birth, and the latter is, as Huxley and Dollo suggest, in turn dependent upon arboreal habit, then already in the Jurassic period the marsupials must have had their special characters well under way; so that the common ancestors of marsupials and placentals must be placed, as Osborn has indicated, at some time prior to the Jurassic period. Naturally this gives us no clue to a placental or non-placental origin of marsupials, but the distinction, if valid, is an important one, because it avoids the confusion which would result from an attempt to identify and characterize the common ancestors among the more complex faunas of later periods. But more especially it minimizes the importance of the arboreal characters of the marsupials of later periods and renders necessary a knowledge of the foot structure of Jurassic forms before decisive proof of arboreal ancestry may be obtained.

---

[1] Following Gill's division of 1872 (*cf.* Gill, **'72**). The Eutheria as defined by Gill are not assigned a placental or non-placental character. Hence they may be interpreted as equivalent either to the Metatheria of Huxley or to his Eutheria as interpreted by Wilson, Hill, and Dollo.

2. *The Question of a Polyphyletic Origin of the Mammalia.*

As indicated above, the view of Dollo, Wilson, and Hill opposes that of Huxley merely in reversing the relationships of marsupials and placentals while retaining the idea of a general continuity of the Mammalia. The views of other writers, on the other hand, substitute for continuity an independent origin and development of the main mammalian stems.

---

[1] Proposed in 1888; *cf.* opposite opinion of Flower and Lydekker ('**91**, p. 113).

Among the latter there is notably that of Hubrecht (**'95**), which recognizes a polyphyletic origin of the Mammalia from viviparous Amphibia.

Whether or not the embryological data on which Hubrecht bases his conclusions justify this interpretation is a question on which the writer does not feel competent to express an opinion. It may be noticed, however, that Hubrecht's results are differently interpreted by Assheton (**'98**), and that his hypothesis has not been generally accepted.[1]

Hubrecht cites in support of his hypothesis the results of Gegenbaur (**'86**), Mivart (**'88**), Osborn (**'93**), and Klaatsch (**'92**). These may accordingly be examined at the same time in relation to the view of Hubrecht and that of Huxley.

In the first place, Hubrecht regards the recognition by Gegenbaur and Mivart of a fundamental difference between the mammary glands of monotremes and those of the higher mammals as implying an independent origin of the two groups. In some respects this is open to a different interpretation. Gegenbaur, while emphasizing the sudoriparous nature of the mammary glands of monotremes as opposed to the sebaceous nature of those of the higher mammals, was fully aware of the limitations of this distinction, since he found on the mammary areas of monotremes some glands of the latter kind. In discussing the bearing of this he says (p. 35): "Aus solchen Verhältnissen des Drüsenfeldes kann man die Entstehung der Mammardrüsen bei Monotremen und den übrigen Säugern sich vorstellen. Bei den Einen ist die eine Drüsenart, bei den Anderen die andere zur Ausbildung gelangt." In other words, he perceived that from a diffuse condition, in which both kinds of glands were present, we may derive the monotreme condition by assuming an exclusive development of one set of glands, and the higher mammalian condition by an exclusive development of the other. The significance of this was later fully appreciated by Klaatsch (**'92**), on the discovery by him of both kinds of glands in the peculiar mammary pouches of artiodactyl ungulates. On page 365 of his paper he speaks of a fundamental correspondence between the artiodactyl ungulates and the monotremes in this respect.

---

[1] A more moderate position on this subject has recently been taken by Jenkinson (**'00**).

Here we may notice the opinion of Wilson and Hill (**'97**, p. 579): "We do not believe that in the long run it will be found possible to maintain the essential dissimilarity of the mammary glandular organ in monotremes." This appears to be the more appropriate attitude.

With regard to the results of Osborn, Hubrecht quotes, among other statements, the following one, which he interprets as indicating polyphyletic origin: "All stem mammals were related in their double succession (of teeth), in their dental formula, and in their primitive molar form. These features point not to a succession, but to a unity of ancestry of the monotremes, marsupials, and placentals."[1]

This involves the broader question as to how convergence of type ought to be interpreted in the Mammalia; for, in addition to the results of Osborn, those of Wilson and Hill (**'97**) confirm convergence in dentition, those of Gegenbaur (**'86**) and Klaatsch (**'92**), convergence in the mammary glands, those of Klaatsch (**'92**, **'95**), finally, convergence in the accessory mammary apparatus. All of these suggest unity of ancestry.

If there were no convergence of type in the structures under consideration, Huxley's hypothesis would immediately become untenable, because it would then be necessary to assume a polyphyletic origin. But if we admit convergence, the chances are equally divided between genetic succession and polyphyletic origin. In order to prove the latter, however, it would be necessary to trace the converging structures back to a pre-mammalian stage. In other words, it would be necessary to prove that in progressive development certain structures diverged in character before the mammalian condition was instituted; because if any structure diverged from a type which was still mammalian, the latter would be regarded as also prototherian. None of the above-named structures have as yet been traced to a non-mammalian type.

---

[1] Osborn (**'93**, p. 20).

Finally, Hubrecht mentions the results of Klaatsch in connection with polyphyletic origin. He quotes from Klaatsch as follows: "Dadurch wird man zu der Annahme gedrängt, dass die Hufthiere sich ganz direkt an jene oben dargestellte Urform der Säugethiere anschliessen, deren hypothetische Vertreter man als Taschenthiere oder Bursalia von den Beutelthieren oder Marsupialia unterscheiden kann. Es wird denkbar, dass die Hufthiere niemals ein Marsupialstadium durchliefen."[1]

If we follow Klaatsch throughout the course of his paper, we find that he recognizes a primary condition of the mammary apparatus consisting of paired mammary pouches lodging the mammary glands. Out of these are formed independently the incipient marsupium of monotremes and the perfect marsupium of marsupials. In the artiodactyl ungulates these pouches show no signs of marsupium formation; they are converted into the tubular teat cavities. He accordingly concludes that the artiodactyl ungulates have not passed through a marsupial stage (Marsupialstadium).

Although this is doubtless a true interpretation, it cannot be regarded, as Hubrecht suggests, as pointing to polyphyletic origin; for it is not our object in contemplating polyphyletic origin to prove that, for example, the artiodactyl ungulates have not passed through a marsupial stage, but that they have not passed through a metatherian stage. The results of Klaatsch confirm that which Huxley, notwithstanding the meagerness of his evidence, perceived, namely that the marsupium is not a transitional character but a special character of marsupials.[2]

We may again refer to the opinion of Wilson and Hill (**'97**, p. 579). Concerning the mammary pouches of Klaatsch they speak as follows: "Such a rudimentary or primitive condition must have been characteristic of the common stock of both Metatheria and Eutheria, and was only a marsupial one in the sense that Echidna is now marsupial." From this it is clear that they do not regard Klaatsch's results as at all indicative of polyphyletic origin.

---

[1] Klaatsch (**'92**, p. 369).

[2] Huxley (**'80**, p. 656).

There are still to be noticed certain phases of opinion which chiefly concern the relationships of the Monotremata. In a recent paper by Osborn (**'99**), to which reference has already been made, we find the Monotremes separated off from the marsupials and placentals, and assigned an independent origin on a basis of their distinctness of organization. A similar view has also been expressed by Seeley (**'96**, **'99**).

Under the circumstances this view has been a most natural one. The tendency of recent research has been essentially towards the revelation of placental characters in the Marsupialia (Wilson and Hill (**'97**), Hill (**'97**)), on the one hand, and the revelation of sauropsidan (theriodont, Seeley) characters in the Monotremata (Semon (**'94**), Seeley (**'96**, **'99**), van Bemmelen (**'98**, **'99**, **'00**), Smith (**'99**), Sixta (**'00**), Hochstetter (**'96**), Ziehen (**'97**)). Thus the two groups have been naturally regarded as genetically distinct. It is probable, however, that in assigning a separate origin to them we overestimate their distance apart: in the first place, on account of the deceptive mask of placental characters which the Marsupialia, especially those of Australia, have assumed; and in the second place, because, while diligent search has been made for sauropsidan characters in the Monotremata, little has been done towards a recognition of the prototherian characters of marsupials. That the latter field is not unproductive may be seen from the discovery by Broom (**'97**), in a fœtal marsupial, of a distinct coracoid comparable to that of the Monotremata, and the recent results of McClure, showing that the numerous variations of the postcaval and related veins in the opossum (*Didelphys virginiana*) are all modifications of a ground type which Hochstetter has shown to be characteristic of the embryonic Monotremata.[1] Moreover, we should not lose sight of the familiar osteological characters which marsupials and monotremes have in common.

Reviewing the evidence as a whole, there seems to be no adequate reason for abandoning Huxley's hypothesis. Many of the facts which have recently come to light are rather confirmatory than otherwise, and many others, which have been regarded as antagonistic, are open to a different interpretation. Since it has not been definitely disproven, and especially since no other view has been advanced which explains all of the facts of the case as well, we may justly regard Huxley's theory as entitled to first consideration, even at the present day.

---

[1] These results were kindly communicated to me by Professor McClure.

COLUMBIA UNIVERSITY, NEW YORK.

BIBLIOGRAPHY.

'98 ASSHETON, R. The Segmentation of the Ovum of the Sheep, with Observations on the Hypothesis of a Hypoblastic Origin for the Trophoblast. *Quart. Journ. Micr. Sci.* Vol. xli, pp. 205–262.

'98 BEMMELEN, J. F. VAN. On Reptilian Affinities in the Temporal Region of the Monotreme Skull. *Proc. Internat. Congr. of Zoöl., Cambridge.*

'99 ——— The Results of a Comparative Investigation concerning the Palatine, Orbital, and Temporal Regions of the Monotreme Skull. *Verh. d. Kon. Akad. van Wetenschappen te Amsterdam.* pp. 81–84.

'00a ——— Über den Schädel der Monotremen. *Zool. Anzeiger.* Bd. xxiii, Lief. 622, S. 449–461.

'00b ——— Further Results of an Investigation of the Monotreme Skull. *Verh. d. Kon. Akad. van Wetenschappen te Amsterdam.* S. 930–932.

'97 BROOM, R. On the Existence of a Sterno-Coracoidal Articulation in a Fœtal Marsupial. *Journ. Anat. Phys.* Vol. xi, N.S., pp. 513–515.

'98 DEPENDORF, T. Zur Entwickelungsgeschichte des Zahnsystems der Marsupialier. *Zoologische Forschungsreisen in Australien und dem Malayischen Archipel.* Bd. iii, Lief. 2, S. 245–402. Jena.

'99 DOLLO, L. Les ancêtres des Marsupiaux etaient-ils arboricoles? *Miscellanées biologiques.* pp. 188–203. Paris.

'91 FLOWER, W. H., AND LYDEKKER, R. Mammals Living and Extinct. London.

'86 GEGENBAUR, C. Zur Kenntniss der Mammarorgane der Monotremen. Leipzig.

'72 GILL, T. Arrangement of the Families of Mammals. Washington.

'97 HILL, J. P. The Placentation of Perameles. *Quart. Journ. Micr. Sci.* Vol. xl, pp. 385–442.

'96 Hochstetter, F. Beiträge zur Anatomie und Entwickelungsgeschichte des Blutgefässsystems der Monotremem. *Zoologische Forschungsreisen in Australien und dem Malayischen Archipel.* Bd. ii, Lief. 3, S. 191–300. Jena.

'89 Hubrecht, A. A. W. Studies in Mammalian Embryology. I. The Placentation of Erinaceus europæus, with Remarks on the Phylogeny of the Placenta. *Quart. Journ. Micr. Sci.* Vol. xxx, pp. 283–404.

'95 ——— Die Phylogenese des Amnions und die Bedeutung des Trophoblastes. *Verh. d. Kon. Akad. van Wetenschappen te Amsterdam.* S. 3–66.

'80 Huxley, T. H. On the Application of the Laws of Evolution to the Arrangement of the Vertebrata, and more particularly of the Mammalia. *Proc. Zoöl. Soc. London.* pp. 649–662.

'00 Jenkinson, J. W. A Re-investigation of the Early Stages of the Development of the Mouse. *Quart. Journ. Micr. Sci.* Vol. xliii, pp. 61–81.

'92 Klaatsch, H. Über Mammartaschen bei erwachsenen Hufthieren. *Morph. Jahrb.* Bd. xviii, S. 349–372.

'95 ——— Studien zur Geschichte der Mammarorgane. 1. Theil: Die Taschen- und Beutelbildungen am Drüsenfeld der Monotremen. *Zoologische Forschungsreisen in Australien und dem Malayischen Archipel.* Bd. ii, Lief. 2, S. 77–188. Jena.

'00 McClure, C. F. W. The Variations of the Venous System in Didelphys virginiana. *Anat. Anzeiger.* (In press.)

'88 Mivart, St. G. On the possibly Dual Origin of the Mammalia, *Proc. Roy. Soc. London.* Vol. xliii, pp. 372–379.

'88 Osborn, H. F. The Structure and Classification of the Mesozoic Mammalia. *Journ. Acad. Nat. Sci. Philadelphia.* Vol. ix, No. 2, pp. 186–285.

'93 ——— The Rise of the Mammalia in North America. *Stud. Biol. Lab. Columbia College.* Zoölogy. Vol. i, No. 2, pp. 1–45.

'99 ——— The Origin of Mammals. *Amer. Journ. of Sci.* Vol. vii, pp. 92–96.

'96 Seeley, H. G. On the Complete Skeleton of an Anomodont Reptile (Aristodesmus rütemeyeri Wiedersheim) from the Bunter Sandstone of Reihen, near Basel, giving New Evidence of the Relation of the Anomodontia to the Monotremata. *Proc. Roy. Soc. London.* 1896. pp. 167–169.

'99 ——— The Origin of Mammals. *Internat. Congr. of Zoöl., Cambridge.* (Printed abstract.)

'94 Semon, R. Die Embryohüllen der Monotremen und Marsupialier. *Zoologische Forschungsreisen in Australien und dem Malayischen Archipel.* Bd. ii, Lief. 1, S. 19–58. Jena.

'00 Sixta, V. Vergleichend-osteologische Untersuchung über den Bau des Schädels von Monotremen und Reptilien. *Zool. Anzeiger.* Bd. xxiii, Lief. 613, S. 213–229.

'99 SMITH, G. E. Further Observations on the Anatomy of the Brain in the Monotremata. *Journ. Anat. Phys.* Vol. xiii, N.S., pp. 309–342.

'97 WILSON, J. T., AND HILL, J. P. Observations on the Development and Succession of the Teeth in Perameles; together with a Contribution to the Discussion of the Homologies of the Teeth in Marsupial Animals. *Quart. Journ. Micr. Sci.* Vol. xxxix, pp. 427–588.

'97 ZIEHEN, T. Das Centralnervensystem der Monotremen und Marsupialier. I. Theil: Makroscopische Anatomie. *Zoologische Forschungsreisen in Australien und dem Malayischen Archipel.* Bd. iii, Lief. I, S. 1–187. Jena.

For references to papers of Röse, Leche, Kükenthal, and others, on the dentition of the Marsupialia, see Wilson and Hill ('**97**, p. 582).

For references to papers of Owen, Caldwell, Selenka, and Semon, on the marsupial allantois, see Hill ('**97**, p. 438).